SOMATOSENSORY DEFICIT IN THE MONKEY PRODUCED BY PARIETO-TEMPORAL DISCONNECTION

By
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DEDICATION

To my father and mother, Mr. and Mrs. Edward J. Keating.

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The disruption of the cortico-cortical connections between the occipital and temporal lobes has previously been shown to produce an inability to discriminate visually food from non-food objects that is characteristic of the Klüver-Bucy syndrome.

The present experiment proposed to test whether the cortico-cortical connections between the parietal and temporal lobe formed a somatosensory system functionally analogous to the occipito-temporal pathways of the visual system. Specifically, it was hypothesized that disconnection of the cortical pathways between the postcentral gyrus and the temporal lobe would produce an inability to distinguish edible from the inedible objects on the basis of tactile cues. Since the disconnection was specifically somatosensory no deficits were expected to occur on a second test in which the animal was allowed to determine edibility using visual cues.

Four of the six rhesus monkeys used in the study underwent a series of three operations designed to disrupt in successive stages the cortical connections between the postcentral gyrus and the temporal lobe. Each of these three subjects received the same three lesions but in different order: unilateral ablation of the postcentral gyrus, contralateral temporal lobectomy, and section of the forebrain commissures. In all four animals this parieto-temporal disconnection produced a temporary inability to distinguish a piece of monkey chow from a steel bolt using tactile cues. The design of the experiment prevents explaining the deficit as a result of generalized surgical trauma, or the effects of any single, or any two operations, but points to the disconnection between the postcentral gyrus and the temporal lobe as being responsible for the deficit. The parieto-temporal disconnection in general did not produce visual deficits or changes in emotional responsiveness.

To compare the parieto-temporal disconnection to a less modality — specific interruption of temporal lobe structures bilateral temporal lobectomies were carried out in two control subjects. This bilateral lesion also caused a tactile deficit of short duration. But unlike the parieto-temporal disconnection this preparation produced, in addition, oral sampling, inability to distinguish food from non-food objects using visual cues, and emotional placidity.

The data support the hypothesis that the temporal lobe is involved in the organization of the somatosensory system in a way analogous to the function it serves for vision. The transitory nature of the tactile deficit needs to be investigated.

INTRODUCTION

Part of the renewed interest in the importance of inter- and intrahemispheric cortical pathways has centered around the attempt to understand the Klüver-Bucy syndrome, that complex of behavioral changes that results from bilateral removal of the temporal lobe structures. Geschwind hypothesized that the inability of Klüver-Bucy monkeys to distinguish food from non-food objects, so called "psychic blindness," resulted from the disconnection of visual-rhinencephalic pathways (1965). Anatomical evidence for such an idea exists in a pathway that projects from striate cortex to the inferior temporal gyrus by way of the cricumstriate cortical belt (Kuypers, et al., 1965). In support of this theory, monkeys with one temporal lobe removed and section of the forebrain commissures showed the "psychic blindness" if visual information was permitted to go only to the hemisphere with the missing temporal lobe (Downer, 1961).

With a series of operations that removed all cortico-cortical connections between the occipital and temporal lobes, Horel and Keating (1969) produced the inability to distinguish edible from inedible objects characteristic of the Klüver-Bucy syndrome (Klüver and Bucy, 1937). The monkeys also showed the placidity that normally follows bilateral temporal lobectomy. Unlike the bitemporal lobectomy animals the deficit of the occipito-temporal disconnection monkeys appeared to be strictly visual in that the disconnection monkeys

were able to "get around" the deficit and successfully discriminate the food objects not only by using the oral investigation typical of the bilateral temporal lobectomy, but also by using tactile cues, a behavior not previously reported to occur in Klüver-Bucy monkeys. Horel and Keating (1969) reasoned that tactile sampling was possible because they had selectively disconnected occipital inputs to the temporal lobe structures. Tactile connections with the temporal lobe were left intact by the disconnection procedure, and tactile cues could be utilized by the monkey to evaluate the edibility of objects presented to him.

There is other evidence of the involvement of the temporal lobes in the organization of tactile information. Parieto-temporal connections are somewhat analogous to occipito-temporal connections. The postcentral gyrus, the primary cortical receiving area for somatosensory information sends projections to the superior temporal gyrus by way of Brodmann areas 5 and 7 in the posterior parietal lobe (Jones, 1969; Ebner; 1963). Lesions in all of these structures produce varying degrees and kinds of somatosensory deficits. Retention of preoperatively learned roughness and tactile form discriminations is impaired by bilateral lesions in the temporal lobe, and relearning of these tasks is more seriously impaired by combined temporal and posterior parietal lesions (Blum, 1951; Blum, Chow and Pribram, 1950). Tactile form and roughness discrimination deficits also result from bilateral lesions of Brodmann parietal areas 5 and 7 (Moffett, Ettlinger, Morton and Piercy, 1967) and bilateral lesions of postcentral gyrus (Orbach and Chow, 1959); tactile form discrimination deficits follow a unilateral postcentral gyrus lesion when the animal is tested with the contralateral hand

(Kruger and Porter, 1958).

The present experiment proposed to test whether the connections between the parietal and temporal lobe form a somatosensory system analogous in its function to the role that the occipito-temporal pathways have been demonstrated to serve for vision. If the somatosensory system is analogous, then the disruption of cortical connections between the postcentral gyrus and the temporal lobe in monkeys should produce animals unable to distinguish edible from inedible objects when they can use only tactile cues. Since the disruption was specifically somatosensory, it was further expected that this preparation would differ from the Klüver and Bucy and Horel and Keating preparations in that the somatosensory disconnection animals would have no visual deficits. Specifically, they would have no difficulty selecting edible objects when they could use visual cues.

The disconnection paradigm has been found to be a sensitive instrument for examining the functional relationship between cortical areas. In this paradigm lesions which by themselves will not produce the behavioral deficit in question sever in successive stages the connections between two brain areas. A behavioral change resulting from the completed sequence of lesions, but not occurring at any previous step, cannot be attributed either to generalized surgical trauma or to the ablation of any one brain area, but points to the disconnection between the two areas as being responsible for the resulting deficit.

The ability to rule out general postoperative trauma permits the examination of changes that occur immediately after the operation

that are normally masked by compensatory processes during the usual recovery period that is allowed in most experiments in order to avoid the effects of nonspecific trauma.

METHOD

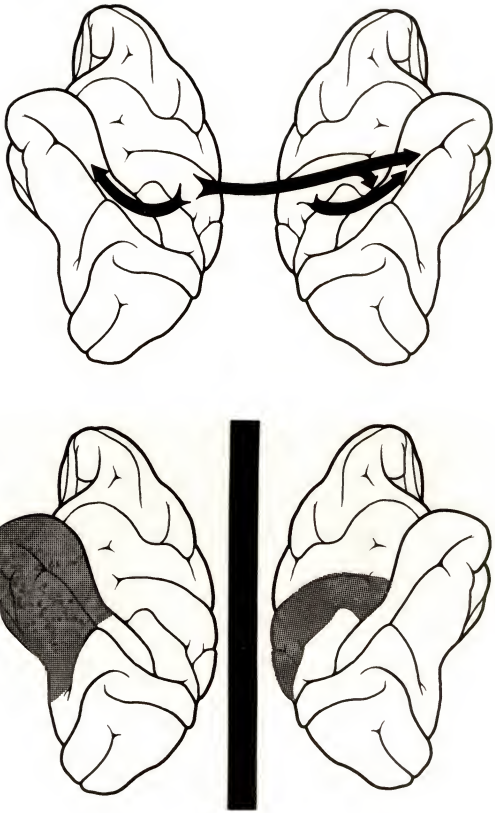
Six adolescent male rhesus monkeys (Macaca mulatta) were used in the experiment. Four of the subjects underwent a series of lesions designed to disconnect in successive stages the cortico-cortical pathways between the postcentral gyrus and the temporal lobe (Figure 1.b). Homolateral connections between these two areas by way of Brodmann areas 5 and 7 have been established in the monkey (Jones, 1969; Ebner, 1963). Heterolateral connections between the postcentral gyrus and the temporal lobe are both indirect: SI projects to contralateral postcentral gyrus (Pandya and Kuypers, 1968), and direct: removal of the entire parietal lobe produces degeneration in the contralateral superior temporal gyrus (Ebner, 1963).

On the basis of this anatomy, a parieto-temporal disconnection for fine tactile information coming from one hand can be produced by either a two-stage or three-stage series of lesions depending on whether or not the cortical somatosensory system is completely decussated. The classical assumption has been that unlike the eye, which projects to both ipsilateral and contralateral cortex, fine tactile information in one hand is controlled completely by the contralateral hemisphere. This view has been generally supported by the lack of interhemispheric transfer of fine tactile information in the absence of forebrain commissures (Kohn and Myers, 1969; Ebner and

FIGURE 1

(A) Schematic diagram of cortical connections between the postcentral gyrus and the temporal lobe.

(B) Sequential lesions designed to disconnect the cortical connections between the postcentral gyrus and the temporal lobe: left temporal lobectomy and right postcentral gyrus ablation destroyed homolateral connections. Forebrain commissure section removed remaining heterolateral connections between surviving left temporal lobe and right postcentral gyrus.



Myers, 1962; Glickstein and Sperry, 1960). In this case, removal of one temporal lobe and subsequent section of the corpus callosum would interrupt all parieto-temporal connections for information arriving over the hand controlled by the hemisphere with the missing temporal lobe. There is some evidence, however, that the cortical somatosensory system is not completely decussated, but that the ipsilateral hemisphere is normally involved or can take over the control of fine tactile information from the hand (Kruger and Porter, 1958; Downer, 1959). The results from the first subject of the present experiment suggested the latter hypothesis of bilateral control of tactile information, and a more radical three-stage disconnection was decided upon for the remaining subjects: unilateral temporal lobectomy, contralateral postcentral gyrus lesion, and section of the corpus callosum and anterior commissure (Figure 1.b). The temporal lobectomy combined in a separate operation with the contralateral postcentral gyrus removal destroyed all homolateral connections between primary somatosensory cortex and the temporal lobe. Remaining heterolateral connections between the surviving temporal lobe and postcentral gyrus were removed by section of the forebrain commissures.

The temporal lobectomy was carried out through a skull opening along the upper edge of the zygomatic arch. To be comparable to lesions in other experiments producing Klüver-Bucy symptoms (Klüver and Bucy, 1937; Horel and Keating, 1969), it extended 2.0 cm. posteriorly from the anterior tip of the middle temporal sulcus and within that area included all of the hippocampus, amygdala, and all neocortex including the banks of the sulci. An attempt was made to spare the visual radiations underlying the superior temporal gyrus. The temporal lobectomy was always carried out on the hemisphere contralateral to the monkey's preferred hand.

The contralateral postcentral gyrus lesion included SI and SII (Woolsey, 1958), and the superior parietal gyrus approximately coincident in the macaque with Brodmann areas 3, 1, 2 and 5 (Peele, 1944). The lesion included the banks of all involved sulci.

Section of the forebrain commissures included the entire length of the corpus callosum, the hippocampus commissure where it lay subjacent to the callosum, and the anterior commissure. Interhemispheric transfer of tactile information across the anterior commissure seemed unlikely in view of the removal of one temporal lobe. However, section of this commissure was included as a safeguard against transfer by way of possible spared medial tissue in the temporal lobe lesion.

In sectioning of the forebrain commissures where retraction of the hemisphere was necessary for visual monitoring of the commissures, care was taken to retract toward the hemisphere that was to receive the postcentral gyrus lesion. The further trauma to this hemisphere produced by retraction was relatively unimportant since the arm controlled by this hemisphere was untestable following the postcentral gyrus lesion.

The operations were carried out in a different sequence for each monkey, according to the following schedule:

Subject K3	Forebrain commissures - left temporal lobe - right postcentral gyrus
Subject K8	Right postcentral gyrus - forebrain commissures - left temporal lobe
Subject K10	Right temporal lobe - left postcentral gyrus - forebrain commissures

Subject K11 Forebrain commissures - right postcentral gyrus - left temporal lobe

These four out of a possible six orders of three lesions allowed for control of the effect of any single or any combination of two lesions.

To compare the above disconnection animals with classical Klüver-Bucy preparations, two additional monkeys received a two-stage bilateral temporal lobectomy. One of these two subjects (K12) received no interoperative testing.

After the above subjects had completed the formal schedule of lesions and had shown complete recovery on both behavioral measures, several of them underwent additional surgery for reasons explained in the Results. Subject K8's temporal incision was reopened, and the lesion extended an additional 5 mm posteriorly into the parietal area in a fourth procedure; in a fifth operation, the inferior parietal gyrus (Brodmann area 7) was removed on the side ipsilateral to the temporal lobe lesion. Subject K9's forebrain commissures were sectioned in a third operation that followed a two-stage bilateral temporal lobectomy. Subject K10 received a fourth operation that removed the occipital cortex contralateral to the lesioned temporal lobe. This, along with the previous temporal lobe lesion and corpus callosum section, completed the occipitotemporal disconnection. The above operations also provided further control for the effects of generalized trauma resulting from extensive surgery.

Animals were operated on under Nembutal anaesthesia following the usual aseptic precautions. All lesions were produced

by subpial aspiration with the aid of a dissecting microscope. Operations on each monkey were performed no sooner than ten days following the previous operation, but as soon after ten days as the animal's health allowed.

Subjects were sacrificed at varying times following their last operation. Verification of the lesions included gross photographs of the lesions and photographs of coronal sections of the tissue cut at 5 mm intervals. Selected areas of the brains were then further sectioned at 30 micron intervals and stained with thionin for finer analysis of the lesions.

Behavioral Measures

All subjects were tested in a modified primate cage to which special trays could be attached (Figure 2). The animals were tested for their ability to distinguish edible from inedible objects when using only tactile cues on one test and when allowed visual cues on a second test. The subject was allowed access to the trays only through two openings, one on either side of the cage. The openings were placed so that the monkey could reach the left side of the tray only with his left hand and the right side with his right hand. The openings were covered by swinging doors, and in this way control for the hand being tested could be maintained without physically restraining the animal's arm.

Visual test. - A flat stimulus tray was attached to the cage (Figure 2.a) and a transparent plexiglass barrier placed between the monkey and the tray. This allowed him to view the objects but prevented him from reaching them except through the openings on either side of the tray.

(a) (b)

FIGURE 2

Testing cage with opening on side of tray controlled by a swinging door.

(a) Flat stimulus tray and transparent plexiglass barrier used on visual test.

(b) Opaque barrier and tray with foodwells used on tactile test.

The food and non-food objects were one raisin and one 1/4-inch square steel nut presented simultaneously on one side of the tray in clear sight of the monkey. They were placed in varying positions on the tray, always separated by 2-1/2 inches. Their position relative to the monkey was randomized according to a modified Gellerman series (Fellows, 1967). At the onset of a trial, the opening to the tray was uncovered, and the order and way in which the subject sampled the raisin and nut were recorded on counters. Responses to the steel nut were categorized as Non-Food Oral (NFO) if he picked it up and brought it to his mouth, or as Non-Food Tactile (NFT) if he picked it up and dropped it without bringing it to his mouth. A trial was considered to last until S had eaten the raisin. His responses to the steel nut were then recorded for an additional 20-second post-trial period.

Tactile test. - A tray with four foodwells, one pair on each side, was used (Figure 2.b). The foodwells were one inch in diameter and one-half inch deep. The wells in a pair were separated by one inch from each other, their centers set 1-1/2 inches from the edge of the tray and 3-1/2 inches (inside well) and 5-1/2 inches (outside well) from the monkey. An opaque masonite barrier replaced the plexiglass barrier used in the visual tests and concealed the foodwells from sight. The food and non-food objects for this test were a piece of monkey chow, 1/2-inch cubed, and a 3/4-inch long steel bolt. One object was placed in each well, and its position was randomized according to the same schedule used in the visual test. A non-correction procedure was used. The monkey was free to reach around the barrier to palpate the objects in the foodwells, but was

allowed to carry only one object to where he could see it or bring it to his mouth. At that point, closing the door prevented him from returning to the tray and sampling the second object. A conservative criterion defined any object carried beyond the edge of the tray as being within the monkey's line of sight.

When the animal retrieved the steel bolt rather than the food, an error was recorded and differentiated as to whether he carried the bolt to his mouth (oral sampling, NFO) or merely looked at it and dropped it (visual sampling, NFV).

At the beginning of the tactile test each day S was given an adaptation trial to familiarize him with the position of the two foodwells. A piece of monkey chow was placed in each well, and the monkey was allowed to retrieve both pieces of food.

Each hand was tested 10 trials per day on both visual and tactile tests for a total of 40 trials in a daily testing session. Animals were tested daily for at least five days preoperatively and interoperatively, and then until a 90 per cent performance on the tactile test on two consecutive days was achieved. Interoperative testing began on the day after the operation if possible, or as soon after surgery as the animal had recovered sufficiently to perform the test.

In addition to these quantitative measures, daily protocols were kept recording changes in emotionality, motor control, response tendencies or any other day-to-day changes in behavior.

RESULTS

It was hypothesized that the temporal lobe was involved in the organization of somatosensory information in a way analogous to the role it serves for vision. It was further proposed that disruption of cortico-cortical connections between the postcentral gyrus and the temporal lobe would produce tactile deficits. The method of producing this disconnection was to disrupt homolateral connections between the postcentral gyrus and the temporal lobe by destroying one temporal lobe and in a separate operation removing the contralateral postcentral gyrus. The remaining interhemispheric connections between the intact temporal lobe and postcentral gyrus were disrupted by section of the forebrain commissures. It was expected that the most severe tactile deficit would occur following the third procedure which completed the disconnection regardless of the order in which it was done. The term "deficit" will be used loosely to indicate any deviation from preoperative criterion performance. Since each object underwent a different sequence of lesions, each represents a different experimental treatment. The results will be reported individually.

Subject K3

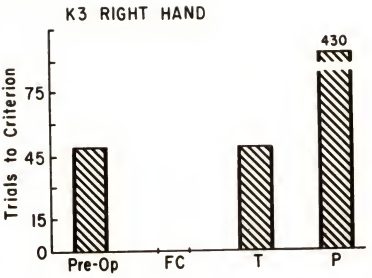
The results of K3's performance on the tactile test following each operation are shown in Figure 3. It can be seen that

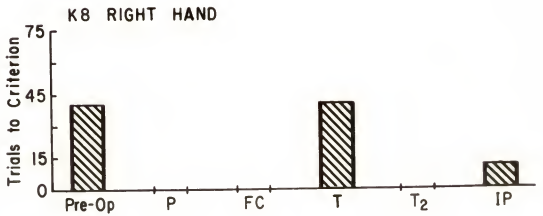
FIGURE 3

Subject K3. Number of trials to criterion on tactile tests preoperatively and following each operation: forebrain commissures (FC), temporal lobectomy (T), and postcentral gyrus removal (P).

FIGURE 4

Subject K8. Number of trials to criterion on tactile test preoperatively and following each of three operations in parieto-temporal disconnection sequence. This subject was also tested after additional surgery, which included an extension of the original temporal lobe lesion (T_2) and removal of the inferior parietal gyrus ipsilateral to the temporal lobe lesion (IP).


K3 RIGHT HAND
Trials to Criterion
0
15
45
75
430
Pre-Op
FC
T
P


K8 RIGHT HAND
Trials to Criterion
0
15
45
75
Pre-Op
P
FC
T
T2
IP

section of the forebrain commissures produced no disruption of his preoperatively learned tactile task. When the left temporal lobectomy was added to the previous commissure section, a number of trials approximately equal to the preoperative learning score was required to reach criterion on the tactile test. Whenever K3 retrieved the steel bolt on this test, he sampled it orally by at least touching it to his lips and frequently putting it in his mouth. This oral sampling persisted until the animal was sacrificed.

After the second operation, K3 also became completely unresponsive to visual threats. Rapid movements and the approach of the experimenter's hand all failed to evoke a startle response. In this, K3 resembled the subjects with bilateral temporal lobe removals and differed from the other parieto-temporal disconnection animals.

It was originally expected, based on the concept of a decussated somatosensory system, that these two operations would complete the parieto—temporal disconnection for tactile information in one hand. The model was partly supported in that this combination of two lesions produced a greater deficit than any other combination of two lesions performed on the other parieto-temporal disconnection animals in the experiment.

When his performance on the tactile test had returned to criterion, a third lesion, removal of the right postcentral gyrus contralateral to the missing temporal lobe, reproduced the tactile deficit on one hand. The other hand, the one contralateral to the postcentral gyrus lesion, was rendered untestable and generally unusable by this operation. In all animals the postcentral gyrus

lesion caused total unresponsiveness to tactile stimuli on the whole contralateral side of the body that recovered partly after one week; a contralateral ataxia which showed very little recovery for as long as the animals were tested was also seen. Except as noted below for K3, the effect was always unilateral and nearly identical for all animals. It will not be described further.

Immediately following the third operation and for the first 20 days (200 trials), K3's performance on the tactile test was random; he retrieved the first object that he palpated in the foodwells. Thereafter, his performance improved and returned to criterion on the 45th day. The third operation, which produced the most severe deficit, was on the hemisphere ipsilateral to the hand being tested, the wrong hemisphere to explain the effect as a result of trauma.

Whereas the combination of forebrain commissure section and temporal lobectomy produced an animal unresponsive to visual stimuli, after the removal of the postcentral gyrus K3 also became unresponsive or only mildly responsive to being stroked or otherwise touched on either side of his body. His mild response was poorly localized and consisted of only a general orientation to the side stimulated.

No abnormalities on the visual test were observed after any of the operations until the 20th day following the third procedure. From that time, K3 evidenced signs of increasing blindness. He misreached for raisins and fished for objects, sweeping his hand back and forth across the tray, picking up whatever he touched. By the 40th postoperative day, he failed to respond to the objects held in front of his face. Visual following could be induced only

for moving objects presented at a distance greater than two feet. Otherwise, he remained active, maintained a good appetite and showed no loss of motor control. His increasing debility seemed restricted to failing vision. This could not be proven conclusively, especially in view of the severe hydrocephaly as evidenced from the enlarged ventricles discovered on post-mortem examination. However, during the same period that he developed near-complete blindness, his performance on the tactile task improved so that by the 45th day he had reached criterion.

Subject K8

Since the largest tactile deficit was seen following the postcentral gyrus removal in K3, an animal (K8) was prepared to control for the effects of this lesion alone (Figure 4). Except for the contralateral ataxia and hypoesthesia already noted, no disruption of either visual or tactile task on the tested right hand or any other behavioral change resulted from the right postcentral gyrus removal alone or when combined with section of the forebrain commissures. The final stage of the parieto-temporal disconnection, a left temporal lobectomy produced a tactile deficit equal to the preoperative learning score (when the amount of deficit is measured as the number of trials to criterion). However, the animal's performance never dropped below 70 per cent, and it returned to criterion on the fifth day of testing.

To investigate if this rapid recovery were due to an incomplete temporal lobe lesion, a fourth procedure extended the original temporal lobectomy 5 mm posteriorly with no effect. A fifth procedure removed on the same side the inferior parietal gyrus

(Brodmann area 7), the parietal area of primary projection to the superior temporal gyrus (Jones, 1969), also with very little effect. Histological verification of the lesions (below) showed them to be comparable in extent and completeness to the ablations in the other parieto-temporal disconnection animals. These additional operations left the question of K8's rapid recovery unsolved. However, they provide further argument against the cumulative effects of surgery as the cause of the tactile deficits seen in the study.

None of these operations produced any visual deficits in this animal. The monkey rarely sampled the inedible object on the tray, and never in preference to the raisin. On the tactile test, when the steel bolt was retrieved, K8 did not sample it orally but threw it away as soon as he was able to see it. There was also no change in emotional responsiveness. He remained normally reponsive to visual threats and to tactile stimulation on the side of his body ipsilateral to the postcentral gyrus lesion.

Subject K10

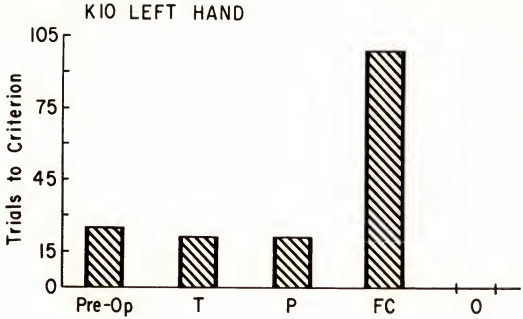
To complete the controls for the effect of any single operation, K10 first received a unilateral right temporal lobectomy, the lesion which, as a third procedure in K8, produced the largest effect. It produced in K10 a tactile retention deficit on the left hand which recovered with some savings (Figure 5). An effect of equal duration returned following the second procedure, a left postcentral gyrus ablation. Again the largest deficit, approximately five times the deficit occurring following the first or second operations, was produced by the third stage of the

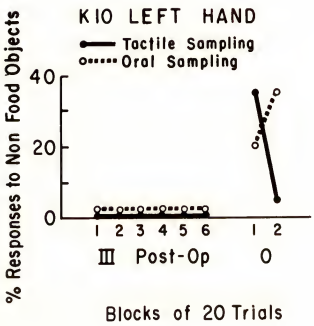
FIGURE 5

Subject K10. Number of trials to criterion on tactile test preoperatively and following each operation of parietal-temporal disconnection. Animal showed no impairment of tactile performance following a fourth operation, removal of occipital lobe (O) contralateral to the temporal lobe lesion.

FIGURE 6

Subject K10. Per cent of responses to non-food objects represents percentage of trials in which subject sampled the steel nut prior to the raisin. Addition of tactile and oral sampling measures extent of animal's inability to distinguish the edibility of the raisin from the steel nut. Random performance (50 per cent) indicates complete deficit.


K10 LEFT HAND
105
75
45
15
0
Trials to Criterion
Pre-Op
T
P
FC
0


K10 LEFT HAND
Tactile Sampling
Oral Sampling
40
20
0
% Responses to Non Food Objects
1 2 3 4 5 6
1 2
III Post-Op
0
Blocks of 20 Trials

disconnection, a forebrain commissure section. Retraction of the hemisphere required by this surgery was toward the side ipsilateral to the hand being tested and, therefore, not likely to traumatize control of the tested hand. Furthermore, no traumatic effects from commissure section in other subjects (K3 and K8) were observed when it was carried out as a first or second procedure.

No visual deficits or oral sampling resulted from these three procedures. A slightly exaggerated response to visual threats and tactile stroking were observed after the third operation.

After he had recovered, K10's left occipital lobe contralateral to his already lesioned right temporal lobe was removed in an attempt to compare the parieto-temporal disconnections to the occipito-temporal disconnections reported by Horel and Keating (1969). Since K10's corpus callosum had also been previously sectioned, this fourth procedure completed the occipito-temporal disconnection. Prior to this, K10 had shown no visual deficits (Figure 6). Following ablation of the striate cortex, his performance became random on the visual test for the four days that he was tested (when tactile and oral sampling on non-food objects are added together in Figure 6). He sampled whichever object was closest to him. He showed the persistent oral examination of objects about his cage, including his fecal matter, observed in the bitemporal animals of this study as well as the tactile sampling of test objects reported for the occipito-temporal animals (Horel and Keating, 1969). He became entirely placid and unafraid of visual stimuli after his striate cortex ablation and approached, sniffed at and gently chewed any object presented to him. However, he reacted

to tactile stimuli with a normal startle response. There was no return of tactile deficit following his fourth operation. Separable tactile and visual disruption of his ability to distinguish food and non-food objects was thus produced by different anatomical disconnections.

Subject K11

Forebrain commissure section in this subject followed by a right postcentral gyrus lesion (Figure 7) completed the controls for the effect of any combination of two operations in the sequence. No effect on his tested right hand resulted from the second operation of this combination. The third operation, a left temporal lobectomy, produced the largest deficit, a negative savings over the preoperative score of about 80 per cent. No change in visual or emotional response was observed in this subject following any of these procedures.

Subject K9 and K12

A second hypothesis of the experiment proposed that the parieto-temporal disconnections described above would result in deficits specific to the somatosensory system. Unlike the bitemporal and occipito-temporal preparations, they were expected to have no visual deficits. Except for the oral sampling of K3, the performance of the disconnection subjects described above bore out this hypothesis.

The less sensory-specific bilateral temporal lobectomies were hypothesized to produce both visual and tactile deficits on these same measures. To test this, subjects K9 and K12 underwent two-stage bilateral temporal lobectomies.

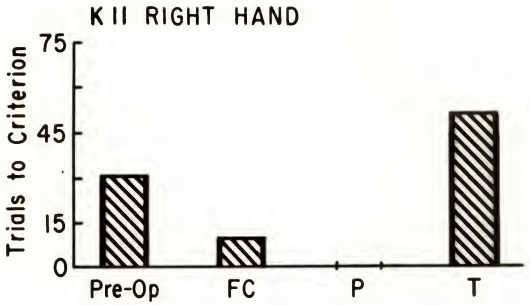


FIGURE 7

Subject K11. Number of trials to criterion on tactile test preoperatively and following each operation.

Subject K9

This subject was tested interoperatively and the unilateral lesion produced no deficits on either hand on either task. His second temporal removal produced both visual and tactile deficits (Figures 8 and 9). He sampled the inedible objects orally and tactually until the sixth postoperative day when his oral sampling was entirely replaced by tactile sampling. Outside of the test situation, K9 continued the oral sampling of objects presented to him.

This subject showed another response on the visual test that the parieto-temporal animals did not share. He always removed both objects from the tray and then responded to the empty tray by placing his hand on it or scratching it. He repeated this repetitious pawing of the tray as frequently as 50 times a trial. Klüver and Bucy (1937) reported this perseverative response for their bitemporal animals.

On the tactile task, the second operation produced a small deficit whose recovery to criterion was equal to the preoperative score (Figure 9). This subject's performance on the tactile test differed from the disconnection animals in that when he retrieved the steel bolt, he sampled it orally before rejecting it.

The bitemporal removal produced the dramatic emotional changes typically reported for these preparations. No visual threat or object could be found which produced a fright response. When the experimenter touched bitemporal K9 on the face and hands, he responded by orally examining the experimenter's fingers. Touching him anywhere else on his body produced at least a mild startle

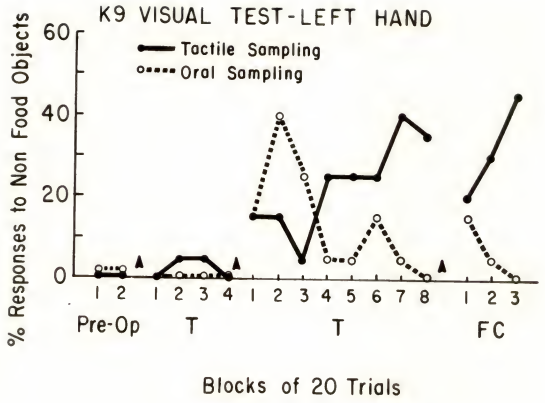


FIGURE 8

Subject K9. Percentage of trials in which subject sampled the steel nut prior to the raisin. Addition of tactile and oral sampling scores measures animal's inability to visually determine the edibility of the objects.

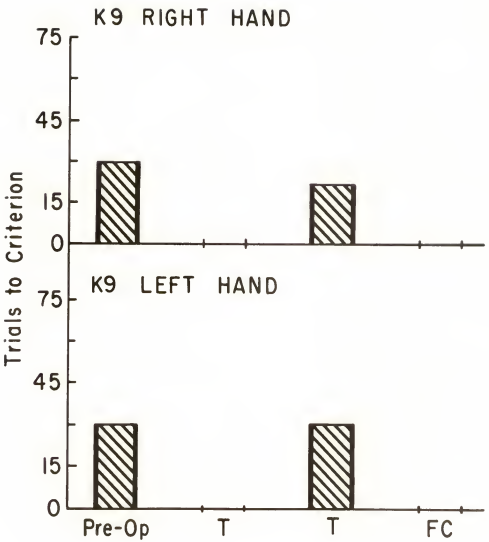


FIGURE 9

Subject K9. Number of trials to criterion on tactile test preoperatively and following unilateral and bilateral temporal lobectomy and section of the forebrain commissures.

and sometimes a squeal of fright. This animal strongly resisted any attempt by the experimenter to restrain him.

Eighteen days after his second operation, K9 had recovered partially on the visual test, and his oral sampling on this test had disappeared. At this time, a section of the forebrain commissures was carried out to see if this procedure would differentiate the hemisphere responsible for the recovery by lateralizing the recovery to one hand. Instead, the temporary elevation of the visual deficit and oral behavior that it produced was symmetric for both hands. No further impairment of the tactile discrimination resulted from this third operation.

Subject K12

To examine whether testing between serial removals of the temporal lobes was a factor in K9's rapid recovery on the tactile test, K12's temporal lobes were removed in two stages, but without interoperative testing. In spite of this, the deficit on the tactile test recovered as quickly as that of K9 (Figure 10). The visual deficits, oral sampling, and emotional changes were identical to those reported for K9 with the exception that recovery of all of these measures occurred sooner than for K9 and in a much shorter time than has been reported for bitemporal animals (Figure 11). The lesions analyzed in more detail below were more extensive than the temporal lobectomies (Klüver and Bucy, 1937) as well as the temporal neocortical lesions (Akert, et al., 1961) reported to have produced these symptoms. No quantitative measures of these visual deficits following bitemporal animals have been reported prior to this study.

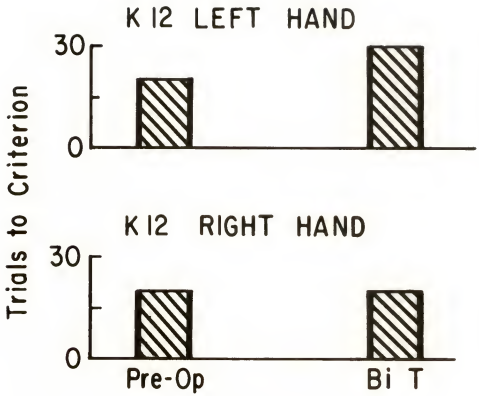


FIGURE 10

Subject K12. Number of trials to criterion on tactile test preoperatively and following bilateral temporal lobectomy (Bi.T.). Performance for each hand is graphed separately.

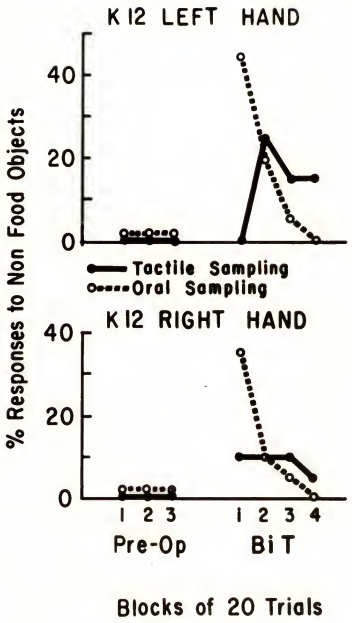


FIGURE 11

Subject K12. Performance on visual test preoperatively and following bilateral temporal lobectomy (Bi.T.). Extent of visual deficit is measured by the addition of tactile and oral sampling scores. Fifty per cent sampling of non-food objects represents complete deficit.

There are verbal reports that the "psychic blindness" and emotional changes continue for many months or even years (Klüver and Bucy, 1937), and also reports of gradual recovery over an unspecified period of time (Akert, et al., 1961).

The results for all animals can be summarized as follows: The hypothesis that disconnection of postcentral gyrus from the temporal lobe would produce a tactile deficit was supported to some extent by the four subjects undergoing this sequence of lesions (Figure 12). In all four animals, the tactile effect following the third operation which completed the disconnection was greater than the effect following any single or any combination of two operations. In three of the four animals, the number of trials to criterion following the disconnection was greater than the preoperative learning score; in K8 the deficit was equal to the preoperative score. The tactile deficit was not dependent on any one order of lesions, although two additional sequences must be tried before complete independence of effect from order of lesions can be established. Additional surgery beyond the disconnection sequence in two animals produced only slight or no further tactile deficits.

In general, the disconnection animals did not orally sample the inedible objects on the tactile test, showed no deficits on the visual test and presented no changes in emotional responsiveness to visual or tactile stimuli. The oral sampling and placidity of K3 was an exception to this.

The two subjects with bilateral temporal lobectomies also incurred tactile deficits comparable to each other and to the smallest deficit produced in the disconnection sequence (K8). In contrast to

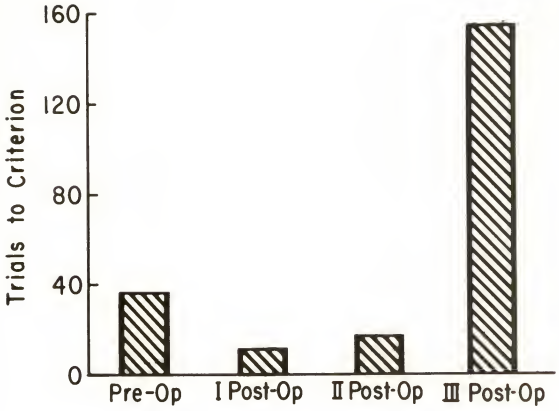


FIGURE 12

Performance (trials to criterion) on the tactile test combined for all four disconnection subjects preoperatively and following each stage of disconnection of the postcentral gyrus from the temporal lobe. The third operation completed the disconnection.

the disconnection subjects, however, bitemporal monkeys showed oral sampling of inedible objects on the tactile test and were severaly impaired in their ability to distinguish edible from inedible objects on the visual test. In further contrast to the disconnection animals, the bilateral temporal lobectomy produced a completely placid response for visual stimuli and the persistent oral sampling of their environment reported by others for this preparation. The effects following the second temporal lobe lesion were not spared by prior interoperative training.

Histology

Photographs of the gross lesions are presented for all animals. Photographs of 30μ celloiden embedded coronal sections stained with thionin are shown for animal K3. Unstained coronal sections of brain cut at 5 mm intervals are presented for the remaining animals. Frozen sections of these animals' brains cut at 25μ were also made through the region of the anterior commissure and part of the dorsal thalamus.

K3 (Figure 13)

Left temporal lobe. - The lesion extended 15 - 18 mm posteriorly from the anterior edge of the middle temporal sulcus. Within that area there was complete destruction of neocortex, including the banks of both sulci, and the hippocampus. A small tag of amygdala was spared (Figure 13.d). The tag of neocortex shown in Figures 13.a and c was found to be completely isolated. Severe hydrocephaly enlarged the inferior horn of the left lateral ventricle, separated the insula from the claustrum (Figure 13.d) and

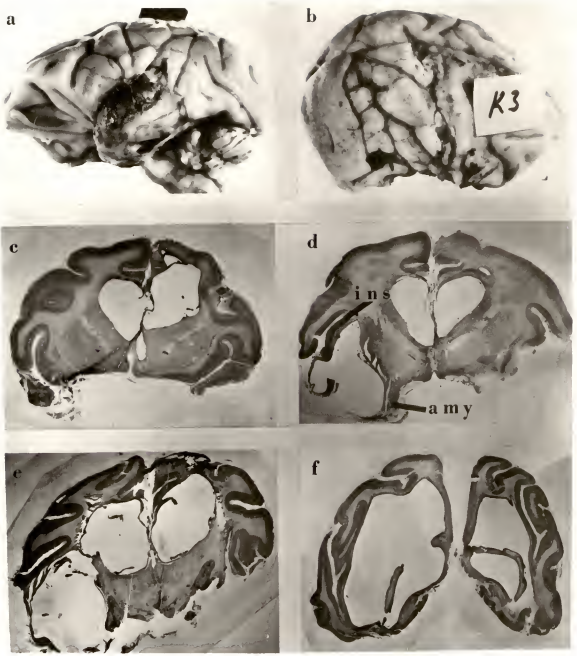


FIGURE 13

Subject K3. Photographs of left temporal lobectomy (a) and right postcentral gyrus lesion (b). Coronal sections embedded in celloidin and stained with thionin (c-f). Legend: amy.-amygdala; ins.-insula.

damaged the striatum. The tail of the caudate could not be traced and was assumed to be destroyed. A strip of cells along the medial edge of both lateral geniculate bodies was degenerated, but the central wedge related to foveal vision appeared healthy.

Forebrain commissures. - The corpus callosum, hippocampal and anterior commissures were completely sectioned. There was a slight invasion of the cingulate gyrus and partial destruction of the left septum at the level of the anterior commissure.

Right postcentral gyrus. - Damage appeared to be complete along the lateral surface of the postcentral gyrus back to the anterior edge of the intraparietal sulcus. The upper bank of the lateral fissure coinciding with SII was completely destroyed. Destruction of the superior parietal gyrus (Brodmann area 5) was no more than 50 per cent complete, as shown in Figure 13.b.

Other damage to the brain included a lesion along the dorsal ridge and medial wall of the right motor cortex. It appeared to be due to pressure from cerebrospinal fluid from the third ventricle trapped under the pia of the right medial hemisphere. The right temporal lobe was also removed, but the animal died on the day following surgery.

K8 (Figure 14)

Left temporal lobe. - Posterior extent of the lesion was 18 - 20 mm and included complete destruction of neocortex and amygdala. A medial strip of hippocampus was spared at the level of the lateral geniculate body. Posterior to that, the hippocampus was completely removed back to its turn toward the midline. The tail of the caudate

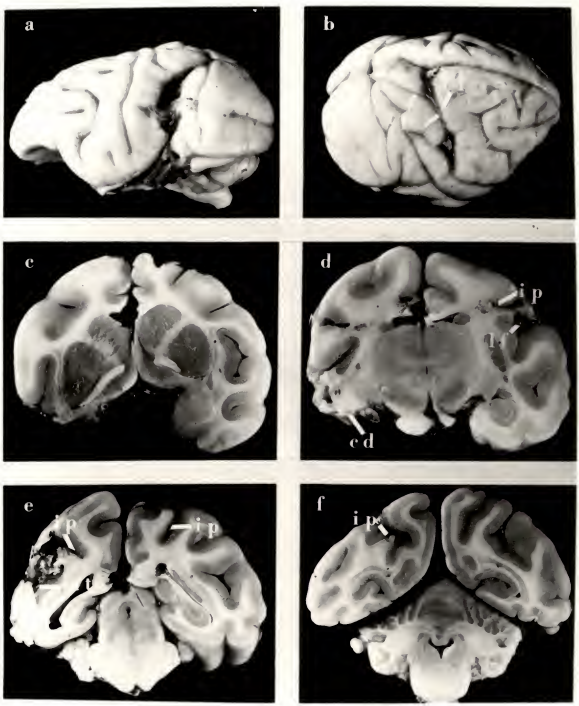


FIGURE 14

Subject K8. Left temporal lobe lesion and subsequent inferior parietal gyrus lesion (a); right postcentral gyrus lesion (b). Coronal sections of unstained tissure cut at 5 mm intervals. Legend: cd.-caudate nucleus; c.f.-central fissure; i.p.-intraparietal sulcus; l.f.-lateral fissure; m.t.s.-middle temporal sulcus.

was destroyed immediately in back of the amygdala, but was spared posterior to that (Figure 14.d).

Right postcentral gyrus. - The extent of the lesion is shown in Figure 14.b. Within that area the involved banks of the central, lateral and intraparietal sulci were included.

Forebrain commissures. - The commissures were completely cut. The left head of the caudate and dorsal thalamus sustained some damage as did the cingulate gyrus (Figure 14.c).

Left inferior parietal lesion. - The inferior parietal gyrus was completely destroyed except for some sparing in the lower bank of the intraparietal sulcus (Figure 14.a and f).

K9 (Figure 12)

Left temporal lobe. - The lesion extended for 26 mm posteriorly to the ventral edge of the lunate sulcus (Figure 15.b). Neocortex, amygdala and hippocampus were completely removed within that area. The tail of the caudate was destroyed back to its rostral turn. The insula was not damaged, although there was slight invasion of the basal ganglia (Figure 15.d).

Right temporal lobe. - The lesion extended for 15 mm posteriorly from the anterior edge of the middle temporal sulcus. Neocortex, amygdala and hippocampus were completely destroyed except for a posteromedial tag of hippocampus (Figure 15). The tail of the caudate was slightly damaged at the level of the lateral geniculates, but was generally left intact for its length.

Forebrain commissures. - All forebrain commissures were completely cut. There was slight damage to the head of the left caudate nucleus and cingulate gyrus (Figure 15.d).

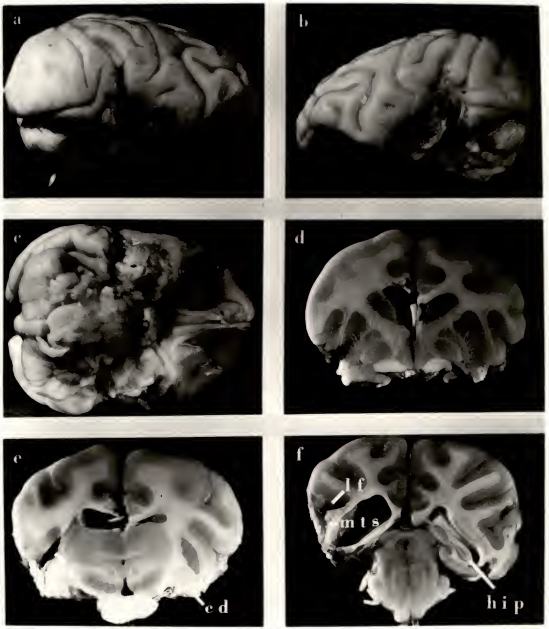


FIGURE 15

Subject K9. Lateral view of right and left temporal lobe lesions (a&b), and ventral view (c). Coronal sections of unstained tissue (d-f). Legend: cd.-caudate nucleus; hip.-hippocampus; l.f.-lateral fissure; m.t.s.-middle temporal sulcus.

K10 (Figure 16)

Right temporal lobe. - The lesion extended 18 mm posteriorly to a point 10 mm anterior to the lunate sulcus (Figure 16.a). There was some sparing of the depths of the superior temporal gyrus (Figure 16.c) and middle temporal sulcus, and a small tag of hippocampus was spared at the level of the lateral geniculate body. The tail of the caudate was heavily damaged and probably destroyed all the way back to its dorsal turn.

Left postcentral gyrus. - SII in the upper bank of the lateral fissure was incompletely removed (Figure 16.e). Destruction of the superior parietal gyrus was complete. Destruction of SI on the medial wall extended posteriorly 5 mm from the postcentral gyrus and ventrally to and including the upper bank of the callosomarginal sulcus.

Forebrain commissures. - All the commissures were completely sectioned. The septum was damaged bilaterally. There was slight damage to the right cingulate gyrus and the left postcommissural fornix (Figure 16.d).

Left occipital lobe. - The striate cortex removal was complete except for the lower bank of the calcarine sulcus. Destruction of the upper bank of this sulcus extended anteriorly all the way to the midbrain.

K11 (Figure 17)

Left temporal lobe. - The lesion extended 18 mm posteriorly to a point along the middle temporal sulcus 7 mm anterior to the ventral tip of the lunate sulcus. The depth of the superior temporal sulcus was spared for 3 mm at the most posterior part of the lesion

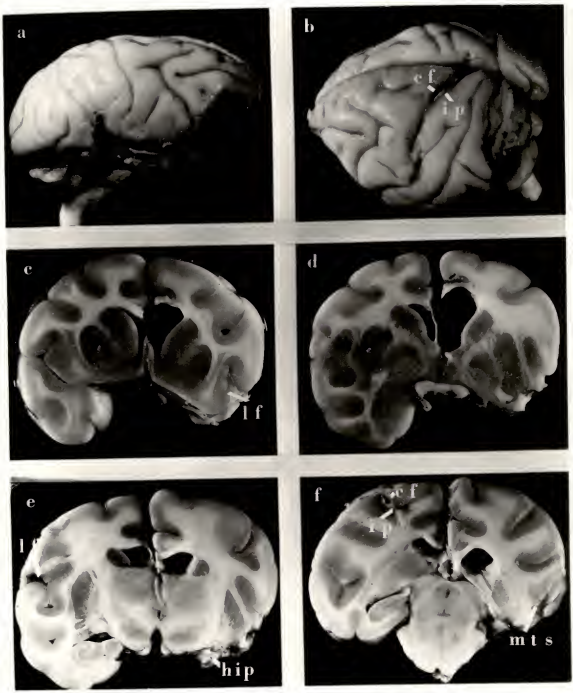


FIGURE 16

Subject K10. Right temporal lobe (a) and left postcentral gyrus lesions (b). Unstained coronal sections (c-f). Legend: c.f.-central fissure; hip.-hippocampus; i.p.-intraparietal sulcus; l.f.-lateral fissure; m.t.s.-middle temporal sulcus.

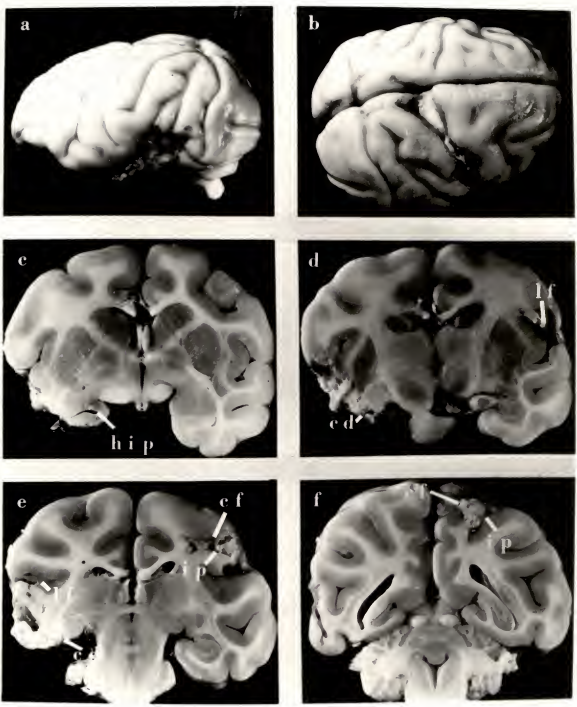


FIGURE 17

Subject K11. Left temporal (a) and right postcentral gyrus lesions (b). Unstained coronal sections (c-f). Legend: cd.-caudate nucleus; c.f.-central fissure; hip.-hippocampus; i.p.-intraparietal sulcus; l.f.-lateral fissure.

(Figure 17.e). A rostral tag of hippocampus extending back to the lateral geniculates was spared (Figure 17.c). The hippocampus was completely destroyed in back of this area to its turn to the midline. The tail of the caudate appeared completely destroyed immediately in back of the amygdala, but only slightly damaged posteriorly through the level of the lateral geniculates (Figure 17.d).

Right postcentral gyrus. - The posterior bank of the central fissure and the intraparietal fissure were destroyed coextensive with the surface area of the lesion shown in Figure 17.b. Sparing in the upper bank of the lateral fissure in Figure 17.d is probably posterior to SII. The posterior part of the superior parietal gyrus was spared.

Forebrain commissures. - The corpus callosum, hippocampal commissure, and anterior commissure were completely sectioned. There was slight damage to the left precommissural fornix and cingulate gyrus (Figure 17.d).

K12 (Figure 18)

Left temporal lobe. - The lesion extended 25 mm posteriorly to the edge of the inferior occipital sulcus. The neocortex was completely removed within that area. There was sparing of the amygdala (Figure 18.c) as well as a medial strip of hippocampus that runs the length of the lesion (Figures 18.d). The rostral tail of the caudate was incompletely destroyed. More caudally it appears to have been completely removed. The insula was not damaged, although there was a slight invasion of the striatum (Figure 18.d).

Right temporal lobe. - The posterior extent of the lesion

FIGURE 18

Subject K12. Right and left temporal lobe lesions (a & b). Unstained coronal sections (c-f). Legend: amy.-amygdala; cd.-caudate nucleus; hip.-hippocampus

measured 25 mm back to the inferior occipital solcus. Neocortical removal was complete. There was some sparing of the amygdala (Figure 18.c) and a rostral tag of medial hippocampus (Figure 18.d). The tail of the caudate was destroyed except for a small dorsal strip at the level of the lateral geniculates. The striatum was invaded, as shown in Figure 18.d.

DISCUSSION

The results shed further light on the orality originally described in animals with both temporal lobes removed. Klüver (1951) suggested that the orality was due to a change in taste preference or a need to supplement the animals' diet caused by a disturbance of metabolism. Taste preference and metabolic changes do result from temporal lobe lesions (Weiskrantz, 1960; Klüver, 1951; Pribram and Bagshaw, 1953). Geschwind, on the other hand, hypothesized that the orality resulted from a disruption of visual-rhinencephalic pathways (1965). The animal used his intact oral system, which presumably does not require forebrain circuits and is not disrupted by temporal lobe damage, to ascertain whether or not the objects were edible. The experiment of Horel and Keating (1969) and the present results support to some extent the latter hypothesis that the oral syndrome is an attempt by the animal to gain sensory information in the absence of visual and tactile cues. In the Horel and Keating experiment visual but not tactile information was excluded from the temporal lobes. The animals sampled the objects orally, but later learned to use tactile cues. In the present study an attempt was made to remove tactile information from the temporal lobe with only partly analogous results. There was a temporary tactile deficit following the disconnection which

the animals were able to "get around" by using visual cues. However, the tactile effects were of shorter duration than the visual deficits usually reported to follow bilateral temporal lobectomies. Rerouting of information (discussed below) between the intact parietal and temporal lobes might possibly explain the transitory nature of the deficit in these subjects. Somewhat more disconcerting, however, was the fact that bilateral temporal lobectomies produced tactile deficits that were no longer in duration than those of the disconnection subjects. Tactile deficits recovered before the visual effects produced by the lesions in both of these bitemporal animals.

Although more transient than the visual deficits, the tactile effects seem clearly to be caused by the disconnection of postcentral gyrus from the temporal lobe. It is hard to explain the data by any other model.

Based on the anatomy of the cortex that has emerged in the past few years, it is not surprising that the temporal lobe should be involved in the processing of tactile information in a way similar to its role in vision. Some studies have reported that no tactile deficits result from temporal lobe lesions (Pasik, Pasik, Battersby and Bender, 1958; Wilson, 1957), but these negative results primarily involved damage to the inferotemporal cortex, and neither study included extensive lesions with even moderate bilateral damage to the superior temporal gyrus or other temporal lobe structures. Furthermore, these, like most studies employing symmetric bilateral lesions, may have missed effects that immediately followed the operation, but that had recovered by the time the animal was tested.

The disconnection paradigm allows for analysis of such deficits by controlling for the effects of postoperative trauma.

Precise delineation of the pathways or critical substructures within the lesioned areas is not possible from these data. The damage was too varied and the number of animals too few to correlate differences of effect with extent of damage to any one or several areas. Research since 1937, generated by Klüver and Bucy's description of the bitemporal animals, has still not factored the symptoms and clearly allocated them to differentiable systems within the temporal lobes. Destruction of the amygdala is probably related to the placidity seen in bitemporal animals (Rosvold, Mirsky and Pribram, 1954), although the relationship is a complex one (Goddard, 1964).

The temporal lobe structures involved in the inability to discriminate food and non-food objects are even less clear. Neocortical lesions which produce visual pattern discrimination deficits typically do not produce "psychic blindness," but more extensive neocortical lesions may produce it (Akert, Gruesen, Woolsey and Meyer, 1961), particularly if bilateral hippocampal damage is included (Mishkin and Pribram, 1954). Amgdaloid-hippocampus lesions which spare the temporal neocortex reproduce some of the Klüver-Bucy symptoms, but not the psychic blindness (Pribram and Bagshaw, 1953). Visual discrimination deficits comparable to those resulting from inferotemporal lesions have resulted from stereo-taxic lesions in the tail of the caudate (Divac, et al., 1967). This structure may also prove to be involved crucially in the monkey's inability to distinguish food from non-food objects.

Several possible explanations can be offered for the recovery of both visual and tactile deficits that took place in these animals.

The hypothesis of selective sensory disconnections makes it attractive to suppose that the animal relearned the task using a different sensory system than the disconnected one. The non-correction method punished attempts to sample on the basis of visual cues. Masking of auditory cues with felt lining in the foodwells did not disrupt the animal's recovery, probably ruling this system out. Perhaps kinesthetic cues based on the finger position around the object or different weights of the objects are part of a gross tactile system not affected by the disconnection and may have been used to relearn the task (Ruch, Fulton and German, 1938). The critical parameters of the stimulus attended to by the Klüver-Bucy monkey have never been worked out even for visual stimuli. The objects on the tactile test differed in size, texture, weight, and form, and it would be impossible to specify the exact somatosensory cue originally learned or used to recover.

Recovery could also be due to incomplete cortical disconnection caused by sparing of frontal, parietal, or, less likely, temporal lobe tissue. The temporal lobe lesions on all animals were as extensive as previous bitemporal lesions and occipito-temporal disconnections producing Klüver-Bucy symptoms. Most of the parietal lesions were complete for SI and SII. However, it is notoriously difficult to produce lasting tactile deficits with extensive parietal lobe lesions (Moffet, et al., 1967). Kruger and Porter found that recovery of tactile deficits occurred unless the ablation of pre-

central gyrus was included along with complete ablation of SI and SII (1958).

Preoperative overtaining (Orbach and Fantz, 1951), seriatim removals combined with interoperative training (Thompson, 1960; Kircher, Braun and Meyer, personal communication; Meyer, Isaac and Mahr, 1958) and general home-cage exposure to the food objects used in the test (Chow, 1952) may also have hastened this recovery. Rerouting of information from the intact parietal lobe to the surviving temporal lobe, perhaps through subcortical pathways, is another possibility. Some reorganization of somatomotor hand control involving ipsilateral somatosensory cortex was observed in K3. A forebrain commissure section followed by a left temporal lobectomy produced a tactile deficit in his right hand that recovered after six days. The deficit returned to his right hand following a subsequent right postcentral gyrus ablation. This one animal provides limited support for the thesis that somatomotor control of the hand can be directed to some extent by the ipsilateral hemisphere (Sperry, 1968; Kruger and Porter, 1958). Ipsilateral takeover of hand control in the absence of forebrain commissures has also been demonstrated for visuomotor coordination (Downer, 1959). The order of lesions in the other animals did not allow for further test of this effect.

It seemed surprising that the bilateral temporal animals recovered from their tactile effects more quickly than the disconnection monkeys, although it cannot be concluded that the bilateral temporal lobectomy should necessarily cause a more severe deficit than the disconnection sequence which involved only one

temporal lobe. The relationship between unilateral and bilateral lesions is not a simple one. Unilateral lesions have been shown both to enhance performance of a discrimination (Boles and Sheridan, 1969) and to cause deficits which can be alleviated by subsequent contralateral lesions (Sprague, 1966). It is more difficult to explain why the bitemporal animals in the present study recovered from their oral tendencies and partly recovered from their inability to distinguish edible and inedible objects on the formal visual test in so much shorter time than the bitemporal subjects reported by Klüver and Bucy and the occipito-temporal disconnection subjects of Horel and Keating. The present bitemporal monkeys continued their oral examination of objects outside the test situation after they had recovered on the formal test, suggesting that it was the test situation itself that facilitated the substitution of tactile and visual cues in differentiating the edibility of objects. Further experiments will have to elucidate this point, but the information at hand suggests that temporal lobectomy produces most prominently a visual deficit with a less severe tactile deficit, and the two together normally produce the transient oral syndrome in which oral cues are used to differentiate edibility.

The lack of dramatic emotionality changes in the parieto-temporal preparation compared to bitemporal and occipito-temporal monkeys also needs more thorough investigation. Gross tactile information, such as results from being stroked with the blunt end of a pencil, may be controlled by anatomical systems different from those controlling discrimination of tactile patterns and not be affected by cortical lesions (Ruch, Fulton and German, 1938). The results of

such a test are not analogous to the occipito-temporal's placid response to visual stimuli which is tested by the presentation of visual forms known to be cortically controlled. A more comparable somatosensory test of emotionality changes might measure the conditioned emotional response to differentially reinforced tactile patterns.

The experiment attempted and partially succeeded in demonstrating that the temporal lobe's involvement in the somatosensory and visual system is to an extent analogous. The analogy is so far only very general. Many of the somatosensory measures used in parietal lobe lesion studies might be used in conjunction with the disconnection paradigm to re-examine the temporal lobe's somatosensory function. Further analogies with the temporal visual system could then be supported or discarded. It would also be valuable to extend the parieto-temporal disconnection to whatever structures, e.g., precentral gyrus, that are required to produce more permanent tactile deficits and thus shed light on the course of recovery in the present study.

Finally, the experiment attached some functional significance to the intra-cortical pathways between two brain areas. The anatomy of the cortex suggests numerous other connections whose significance may be similarly tested; e.g., the olfactory-temporal connections, and the projections with the frontal lobes maintained by all the sensory modalities represented in the cortex.

SUMMARY

The disruption of the cortico-cortical connections between the occipital and temporal lobes has previously been shown to produce an inability to discriminate visually food from non-food objects that is characteristic of the Klüver-Bucy syndrome.

The present experiment proposed to test whether the cortico-cortical connections between the parietal and temporal lobe formed a somatosensory system functionally analogous to the occipito-temporal pathways of the visual system. Specifically, it was hypothesized that disconnection of the cortical pathways between the postcentral gyrus and the temporal lobe would produce an inability to distinguish edible from inedible objects on the basis of tactile cues. Since the disconnection was specifically somatosensory no deficits were expected to occur on a second test in which the animal was allowed to determine edibility using visual cues.

Four of the six rhesus monkeys used in the study underwent a series of three operations designed to disrupt in successive stages the cortical connections between the postcentral gyrus and the temporal lobe. Each of these three subjects received the same three lesions but in different order: unilateral ablation of the postcentral gyrus, contralateral temporal lobectomy, and section of the forebrain commissures. In all four animals this parieto-temporal disconnection produced a temporary inability to distinguish a piece of monkey chow

from a steel bolt using tactile cues. The design of the experiment prevents explaining the deficit as a result of generalized surgical trauma, or the effects of any single, or any two operations, but points to the disconnection between the postcentral gyrus and the temporal lobe as being responsible for the deficit. The parieto-temporal disconnection in general did not produce visual deficits or changes in emotional responsiveness.

To compare the parieto-temporal disconnection to a less modality — specific interruption of temporal lobe structures bilateral temporal lobectomies were carried out in two control subjects. This bilateral lesion also caused a tactile deficit of short duration. But unlike the parieto-temporal disconnection this preparation produced in addition, oral sampling, inability to distinguish food from non-food objects using visual cues, and emotional placidity.

The data support the hypothesis that the temporal lobe is involved in the organization of the somatosensory system in a way analogous to the function it serves for vision. The transitory nature of the tactile deficit needs to be investigated.

APPENDIX

Number of trials to criterion on tactile test preoperatively and following each operation. Legend: Preop - preoperative testing; FC - forebrain commisure section; P - postcentral gyrus ablation; T - temporal lobectomy; IP - inferior parietal gyrus ablation; O - occipital lobectomy; R - right; and L- left; BiT - Bitemporal lobectomy.

Animal	Lesion	Hand	Trials
K3	Preop	R	50
	FC		0
	LT		50
	RP		430
K8	Preop	R	40
	RP		0
	FC		0
	LT		40
	LT (extended)		0
	IP		10
K10	Preop	L	25
	RT		20
	LP		20
	FC		100
	O		0
K11	Preop	R	30
	FC		10
	RP		0
	LT		50
K9	Preop	L	30
	LT		0
	RT		30
	FC		0

Animal	Lesion	Hand	Trials
K9	Preop	R	30
	LT		0
	RT		25
	FC		0
K12	Preop	L	20
	BiT		30
	Preop	R	20
	BiT		20

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BIOGRAPHICAL SKETCH

Edward Gregory Keating was born on December 2, 1942, in New York City. He attended grammar school there and in California, and graduated from high school in Baltimore, Maryland. He graduated from St. Paul's College, Washington, D.C., with a Bachelor of Arts degree in 1965. After graduation he enrolled at Columbia University for one academic year in order to supplement his undergraduate background in Psychology. In 1966 Mr. Keating was admitted to the graduate studies program of the University of Florida. He received his degree of Doctor of Philosophy with a major in Physiological Psychology in 1970.

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August, 1970

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